

BREEDING BIOLOGY OF THE GADWALL IN NORTHERN UTAH¹

JOHN M. GATES

THE purpose of this paper is to describe the breeding behavior, nesting, re-nesting, and productivity of a population of Gadwalls (*Anas strepera*) studied in the Salt Lake Valley of northern Utah. Published reports of many studies include scattered information on Gadwall breeding biology. Examples are Williams and Marshall (1938), Miller and Collins (1954), and Anderson (1956) on nesting and production; Hammond and Mann (1956) on the ecology of nesting islands; and Sowls (1955) on migrational homing and re-nesting. However, to my knowledge there has not been reported a specific study of the breeding habits of the species.

AREA AND METHODS

Study area.—I made this study from March through August 1956 and 1957, at Ogden Bay Refuge, an artificial marsh located on the delta of the Weber River 12 miles west of Ogden, Utah. This 14,000-acre area was constructed during 1938–46 by the Utah Department of Fish and Game. It was built on flat recession lands surrounding Great Salt Lake, most of which were covered by salt water as recently as 20 years prior to construction (Nelson, 1954*a*: 13). Ogden Bay was created primarily to provide public hunting and to alleviate recurrent outbreaks of botulism in late summer due to unstabilized water levels. Following completion, it also became an important duck-nesting area. Nesting populations increased from 300 breeding pairs in 1941 to a peak of 3,500 pairs in 1953 (Nelson, *ibid.*:67).

At present, Ogden Bay consists of a system of large retaining dikes which impound the Weber River in two separate units. Inside each unit, water is distributed by a secondary system of smaller dikes to provide an interspersion of water with emergent and dry nesting cover. Downstream each unit includes a large, shallow lake serving as a feeding and resting area for migrant waterfowl. A more detailed description of the marsh and an account of the ecological changes in its biota after development is given by Nelson (*ibid.*).

Ogden Bay's elevation is approximately 4,200 feet. Its climate is semiarid; annual precipitation over a 40-year period averaged 14 in., a mean monthly low of 0.51 in. falling in July and a high of 1.72 in. falling in February. Its mean annual temperature over the same period was 64 F, with recorded ex-

¹ Contribution of the Utah Cooperative Wildlife Research Unit: U.S. Fish and Wildlife Service, Wildlife Management Institute, Utah Department of Fish and Game, and Utah State University cooperating.

tremes of -25 F and 106 F. Growing seasons average 160 days in length (U.S. Dept. Agr. Yearbook 1941).

I chose a 450-acre area in the northeast corner of the Unit 1 impoundment for my intensive studies of Gadwall nesting. The study area is an upland tract, but includes a number of seasonally flooded and permanent ponds, and is transected by numerous small ditches and a former channel of the Weber River. High ground during the spring runoff is limited largely to channel and dike banks which support rank growths of upland forbs and grasses. This cover type, 10 per cent of the area, is heavily used for nesting, especially early in the season when water levels are still high. Common cattail (*Typha latifolia*), 24 per cent, and bayonet-grass (*Scirpus paludosus*), 5 per cent, occupy low areas that remain wet throughout the growing season, and spike-grass (*Distichlis stricta*), 41 per cent, dominates intermediate elevations between upland and emergent aquatic vegetation. About 20 per cent of the area consists of temporary and permanent ponds and ditches.

Approximately 40 pairs of Gadwalls bred on the area during each year of the study. Waterfowl nesting there in order of decreasing abundance were: Cinnamon Teal (*Anas cyanoptera*), Gadwall, American Coot (*Fulica americana*), Mallard (*A. platyrhynchos*), Shoveler (*Spatula clypeata*), Pintail (*Anas acuta*), Redhead (*Aythya americana*), Blue-winged Teal (*Anas discors*), Ruddy Duck (*Oxyura jamaicensis*), and Canada Goose (*Branta canadensis*).

Methods.—My study was based primarily on observation of marked hens. I trapped nesting hens with nest traps described by SOWLS (1955:5-6) and marked them individually with multicolored, "Koroseal"-plastic neck tags of the type designed by TABER (1949). Eighty-three hens, including 17 nest-trapped outside the study area, were marked during the study.

Marked hens provided information on brood movements and reneating in 1956 and reneating in 1957. Fifteen 1956-tagged hens that returned in 1957 provided data on migrational homing and breeding-pair behavior. In 1957, to study reneating, I disrupted nests of marked hens at various stages of egg laying and incubation to simulate nest destruction.

I located nests by walking channel and dike banks and by dragging a long rope over nesting cover. I made observations of breeding pairs from an elevated blind on the nesting-study area. I took weekly censuses on the entire marsh during the spring migration and on the nesting-study area during the breeding season. Brood counts were made on the Unit 1 impoundment.

SPRING ARRIVAL

Spring migration.—Spring migration during 1956 and 1957 followed the same pattern (Fig. 1). Gadwalls first appeared in early March. Early arrivals

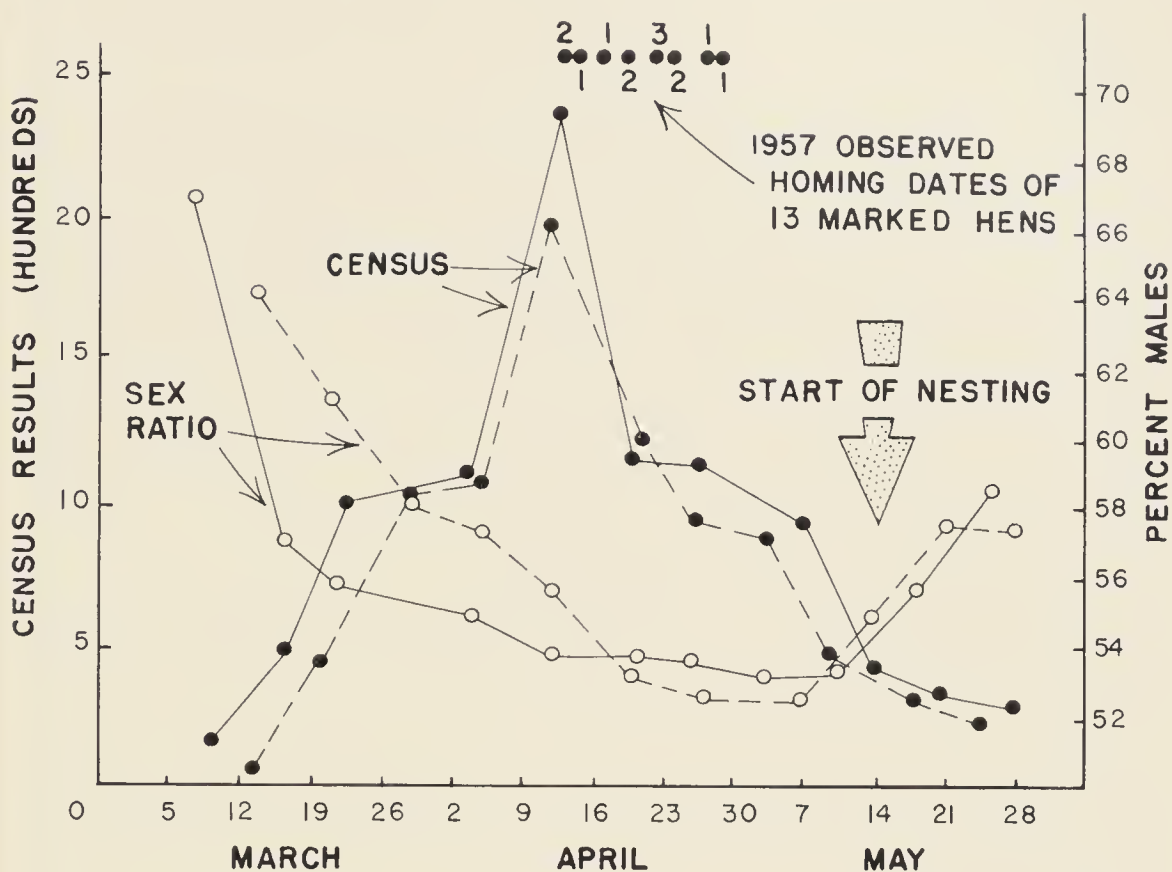


FIG. 1. Results of weekly spring censuses of Gadwalls at Ogden Bay Refuge, 1956 and 1957. Solid lines refer to 1956 data, broken lines refer to 1957 data.

were mostly unpaired and made up largely of drakes. The main passage of Gadwalls occurred during a short period in mid-April and was composed almost exclusively of mated pairs. In both years, spring migration was finished by mid-May. Continued declines in weekly census results after mid-May occurred as some pairs moved to nesting habitats not censused, and others left the marsh to breed on surrounding farmlands. An increased evidence of drakes after mid-May was due to the start of nesting and the onset of territorial behavior. Resident populations of Gadwalls on the marsh eventually numbered 210 and 208 pairs for 1956 and 1957, respectively (Nelson, 1956, 1957).

Gadwalls were among the last ducks to reach Ogden Bay in spring. The chronology of spring migration peaks observed during the study was Mallards and Pintails in late March; Cinnamon Teal, Redheads, and Lesser Scaup (*Aythya affinis*) in early April; Gadwalls in mid-April; followed by Blue-winged Teal and Ruddy Ducks in late April.

Arrival of residents.—Fifteen hens nest-trapped on and adjacent to the study area in 1956 returned in 1957, 13 of which I identified before the start of nesting. Resident hens apparently arrived with the main spring flight of

Gadwalls that occurred in mid-April (Fig. 1). Each of the 13 marked hens was paired at arrival.

The return of adult hens in this study was not in accord with Sowls' (1955: 13-17) findings. At Delta, Canada, he found that Mallards and Pintails which later nested on his area were the first to arrive in spring. The arrival of residents preceded the main flight of migrants by as much as a week. Disagreement between Sowls' findings and those of my study is difficult to explain. Possibly the difference in latitude between Delta and northern Utah, or the differences in species studied are involved. Few Gadwalls were known to winter at Ogden Bay, but the area's close proximity to major Gadwall-wintering areas in central California (Jensen, 1949) might somehow account for the departure from the pattern of spring arrival observed by Sowls on a study area more distant from wintering areas.

Migrational homing.—Fifteen (29 per cent) of the 52 nesting hens marked in 1956 nested at Ogden Bay again in 1957. This does not indicate the actual rate of homing, however, since no allowance is made for the number of hens that did not survive between years.

I have estimated the annual survival rates of Gadwalls from northern Utah by arranging 87 recoveries of 831 Gadwalls banded in the Salt Lake Valley between 1929 and 1953 (344 banded at Bear River Refuge by the U. S. Fish and Wildlife Service, and 414 at Ogden Bay Refuge and 73 at Public Shooting Grounds by the Utah Department of Fish and Game) in a dynamic life table (Hickey, 1952) (Table 1). The bandings consisted of flightless young caught in late summer and of birds treated for and fully recovered from botulism. Many of the latter group were unaged at banding. Thus it was necessary to consider recoveries of aged and unaged birds separately and to omit first-year recoveries of unaged birds from the calculations.

The actual 1956-57 rate of homing is calculated at 60 per cent, based on 48 per cent as the expected survival rate of adult hens (Table 1). I regard this as a minimal estimate of the rate of homing, since it is unlikely that every returning hen was found. In addition, I knew of four individuals that lost neck tags between nesting seasons, and the actual loss of tags probably was even greater. However, it is apparent that at least a majority of the surviving hens marked in 1956 returned in 1957. Sowls (op. cit.:31) observed similarly high rates of homing for adult Gadwall, Pintail, and Shoveler hens at Delta.

Adult hens eventually returned to the immediate vicinity of their original nest (= trapping) sites. The distances between 1956 and 1957 nest sites of 11 marked hens on the study area averaged only 365 yards, with extreme distances of 205 and 510 yards observed.

No information was gained in this study concerning the homing of drakes or juvenile hens. Sowls (ibid.:34-39), however, found the over-all rate of

TABLE 1
CALCULATION OF AVERAGE ANNUAL SURVIVAL RATES OF GADWALLS FROM BANDING IN
SALT LAKE VALLEY, UTAH, 1929-53

Year after banding	No. reported shot		No. alive at start of year		No. alive at end of year	
	Banded as juveniles	Banded as adults or unaged	Banded as juveniles	Banded as adults or unaged	Banded as juveniles	Banded as adults or unaged
0-1	41	—	61	—	20	—
1-2	8	17	20	26	12	9
2-3	5	3	12	9	7	6
3-4	4	4	7	6	3	2
4-5	2	2	3	2	1	0
5-6	0	0	1	0	1	0
6-7	0	0	1	0	1	0
7-8	0	0	1	0	1	0
8-9	1	0	1	0	0	0
Totals	61	26	107	43	46	17
Totals exclusive year 0-1	20	26	46	43	26	17

$$\text{Juvenile survival rate} = \frac{20}{61} = 33 \text{ per cent.} \quad \text{Adult survival rate} = \frac{26 + 17}{46 + 43} = 48 \text{ per cent.}$$

homing of juvenile hens of five species (Pintail, Mallard, Gadwall, Shoveler, and Blue-winged Teal) to be less than a third of that of adult hens. The ties to a specific nesting area which account for homing apparently are largely dependent upon a hen having nested there. In passeriforms also, Hickey (op. cit.:16-17) has pointed out the lower rate of homing of juveniles as compared to adults.

NESTING

Prenesting activities.—Resident Gadwalls arrived at Ogden Bay in mid-April (Fig. 1); however, large-scale nesting was delayed nearly until mid-May (Fig. 2). In 1956 and 1957, known first-egg dates were 1 May and 5 May, respectively. The interval between spring arrival and start of nesting, determined by back-dating nest histories of marked hens to first-egg dates, amounted to nearly a month in 1957 (Table 2). This delay consisted of a postarrival period of 17 days between spring arrival and establishment on a breeding home range (or territory) and a prenesting period of 11 days between the latter and start of egg laying.

TABLE 2
PRENESTING RECORDS OF 13 MARKED ADULT GADWALL HENS, OGDEN BAY REFUGE, 1957

Observed date of spring arrival	Observed date of establishment on breeding home range	Calculated date of first-egg laying
11 April	28 April	9 May
11 April	6 May	16 May
12 April	—	—
15 April	3 May	—
18 April	—	21 May
18 April	12 May	—
20 April	9 May	25 May
20 April	—	9 May
20 April	4 May	15 May
22 April	—	15 May
22 April	7 May	17 May
24 April	—	—
29 April	4 May	14 May

Mean intervals 17 days 11 days

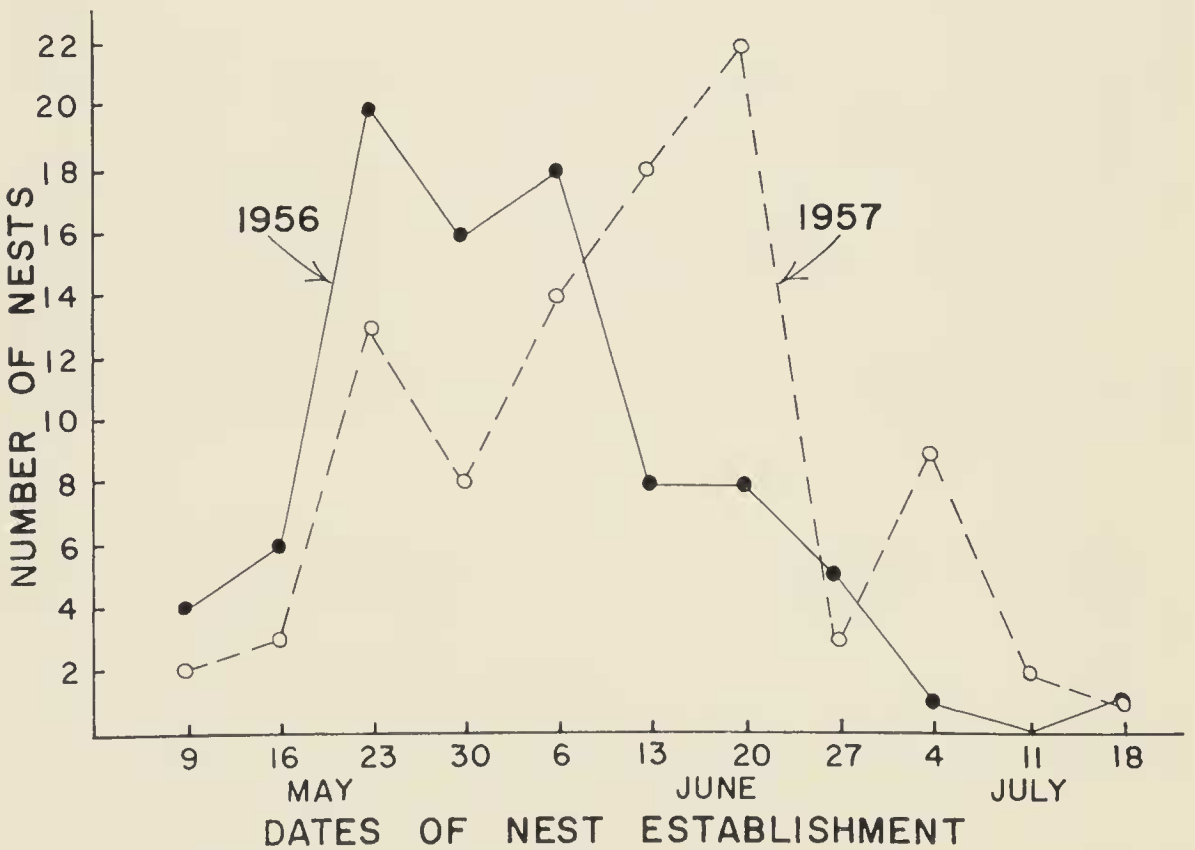


FIG. 2. Phenology of Gadwall nest establishment at Ogden Bay Refuge, 1956 and 1957. The distorted nesting curve in 1957 was the result of re-nesting experiments.

Resident pairs remained gregarious throughout the postarrival period. Usually I found them grouped with other pairs in small flocks of 2–10 which seemingly remained apart from the much larger flocks I considered to be migrants. At this early stage, I observed no sign of nesting behavior or intolerance between pairs.

Six neck-tagged hens were seen twice or more before the start of nesting, providing information on mobility following spring arrival. All were more than a half mile from where they eventually nested, and two hens were sighted nearly a mile and a half away. I observed none in the same area twice, except on what later proved to be their breeding home ranges. Thus it appeared that resident hens were considerably more mobile during the post-arrival period than after they settled down to begin nesting. The nesting-study area, to which all hens originally trapped there eventually returned, was seldom used by Gadwalls before the start of nesting. It was an upland tract, without large feeding and loafing waters on which Gadwalls most commonly gathered in early spring.

Gregariousness ceased and intolerance began when resident pairs established breeding home ranges at the start of the prenesting period. A spacing out of breeding pairs became evident shortly after the earliest pairs took up residence on the study area. I was able to delineate home ranges by plotting the movements of five marked hens and their mates observable from my blind. In each case, breeding home ranges established by marked hens during the prenesting period in 1957 centered closely on their 1956 nest sites (Fig. 3).

In 1957, the movement of breeding Gadwalls onto the study area began in late April and continued until early June (Table 3). However, the eight marked hens (adults) I identified on breeding home ranges were first seen between 28 April and 12 May (Table 2). Thus adult hens were among the earliest to begin nesting. This timing may have been important in their ability to renew residence on specific areas. By being first to establish breeding home ranges in spring, adults probably avoided much of the competition for space occurring later in the season under higher breeding-pair densities which might have interfered with their homing.

Weather conditions during the springs of 1956 and 1957 did not depart from normal. In addition, the phenologies of both spring migration and start of nesting were similar in the two years (Figs. 1 and 2). Accordingly, the timing of Gadwall-breeding events described above appear to be typical for northern Utah.

I am unaware of comparable data on the timing of spring arrival and start of nesting for Gadwalls breeding elsewhere, and thus it is impossible to know whether the near-month interval between the two events observed in this study is characteristic of the species. From Sows' (1955:12, 86) study, it is evident

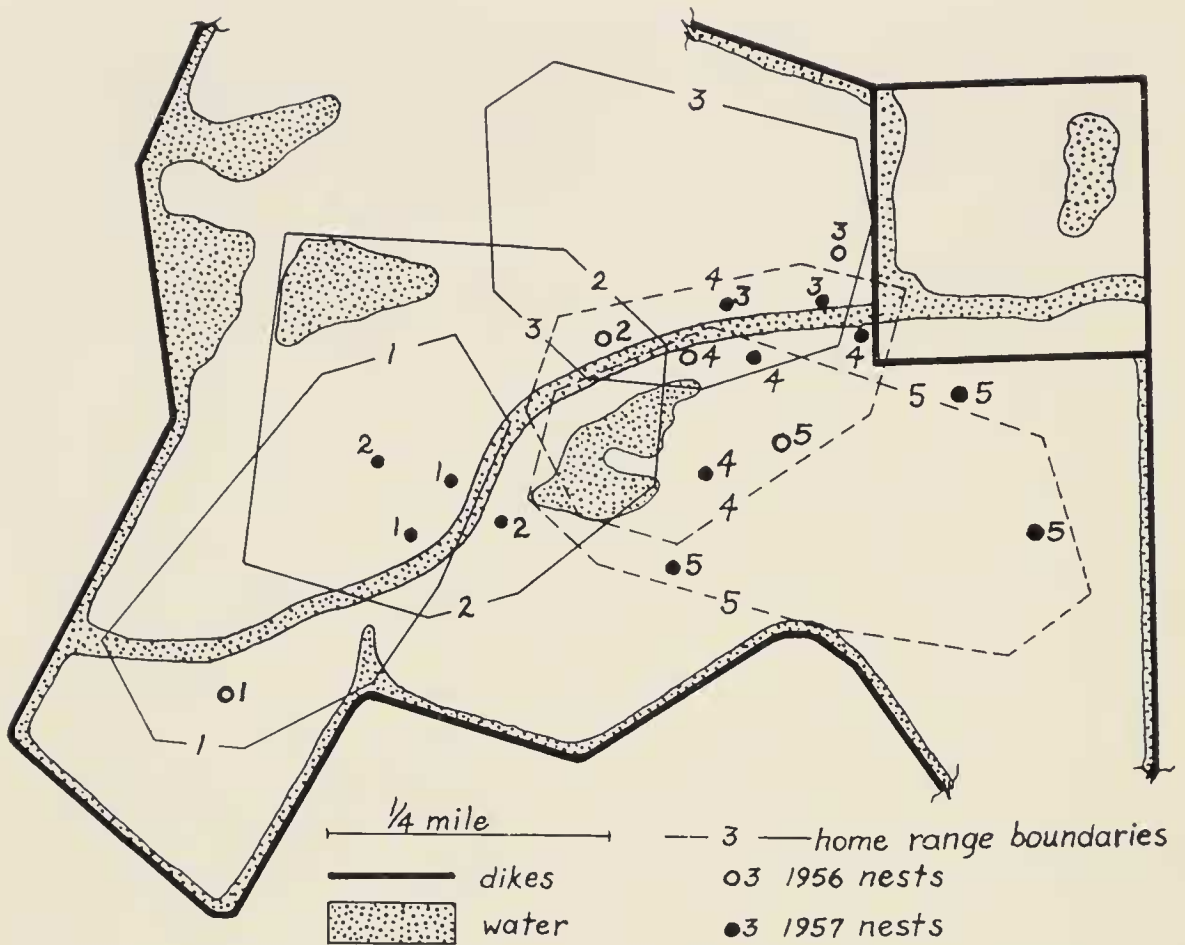


FIG. 3. Breeding home ranges of five marked Gadwall hens during prenesting activities at Ogden Bay Refuge in 1957, showing 1956 and 1957 nest locations.

TABLE 3
RESULTS OF BREEDING-PAIR CENSUSES OF GADWALLS ON STUDY AREA,
OGDEN BAY REFUGE, 1957

Date	Pairs	Lone drakes	Total indicated pairs
25 April	2	0	2
3 May	4	1	5
9 May	11	0	11
16 May	12	5	17
22 May	16	10	26
30 May	9	24	33
6 June	14	27	41
14 June	11	21	32

that at Delta, Mallards and Pintails begin egg laying much sooner after spring arrival. For example, in 1950 the arrival of Mallards and Pintails was 17 April and 19 April, respectively, and nesting of both species began by 30

April. Mallards and Pintails are early nesting species, whereas Gadwalls are among the last of the surface-feeding ducks to began nesting. (At Ogden Bay, Mallards and Pintails started nesting by early April, Cinnamon Teal by late April, and Gadwalls not until mid-May.) Thus I suspect the lengthy delay between spring arrival and egg laying observed in this study is related to the Gadwall's late-nesting habit, and perhaps in turn to its well-known dependence on dry and dense nesting cover (Williams and Marshall, 1938; Miller and Collins, 1954; and others) which becomes increasingly available as spring advances.

Breeding home ranges.—One of Hochbaum's (1944:54–86) conclusions on the breeding behavior of surface-feeding ducks was that at the start of egg laying the hen selected a breeding area which the drake defended as a territory for as long as the pair remained together. The defended area included each of the habitat requirements of the breeding pair, i.e., feeding and loafing areas, water, and nesting cover. The function of the territory was to provide isolation for the breeding pair during the copulation link of the reproductive cycle. Later study by Sowls (op. cit.:47–62) and particularly by Dzubin (1955) resulted in several modifications in this interpretation. They observed that breeding pairs resided on larger, more indefinite areas that they termed home ranges. Home ranges were shared by one or more breeding pairs and were defended only in part. Aggressive behavior often shifted with the movements of the pair and was not limited to specific sites.

In 1957, I observed the behavior and plotted the movements of Gadwall hens marked in 1956. Observations were made on a daily basis largely during prenesting and egg-laying activities. I found that Gadwall behavior followed the pattern of home-range occupancy described by Sowls and Dzubin (Fig. 3).

The general location of the home range was determined by the hen. This was evident from the homing of adult hens, all of which returned to the same areas on which they nested the previous year. Each pair I observed included as part of its breeding home range one or more feeding ponds and a section of channel or ditch used for loafing. Nesting cover was abundantly available on the banks of the many ditches and dikes on the area. Breeding home ranges of five marked hens on the study area during prenesting activities and egg laying varied between 34 and 87 acres in size, averaging 67 acres (Fig. 3). Larger ranges existed on other parts of the marsh where hens had to travel greater distances between water and dry nesting cover. Some Gadwalls nested on farmlands nearly a mile from water.

The breeding home range of a given pair overlapped those of at least several other pairs (Fig. 3). A sharing of breeding areas resulted in that two or more pairs usually used the same pond for feeding or the same part of a ditch

for loafing. However, at a given time a pair was free to use only those parts of its breeding range not already being occupied by other pairs. Two pairs almost never used the same area simultaneously without a display of intolerance on the part of one of the drakes.

The daily ranges of marked pairs I watched were largest in early May. As the number of breeding pairs on the study area built up, the movements of early nesting pairs became increasingly interfered with by the intolerance of other drakes. Apparently in response, these early nesting pairs spent more time at certain favored feeding and loafing areas and attempted fewer flights to outlying parts of their original breeding home ranges. Thus it appeared that early nesting pairs deliberately reduced their daily ranges in order to minimize the number of possible encounters with other pairs. This behavior probably allowed more pairs to breed on the study area than otherwise might have been possible.

During incubation, nesting hens used only the loafing areas and feeding places nearest their nests. Almost all successful hens left the study area soon after the time of hatching. Drakes became less and less faithful to breeding home ranges after their mates began incubating and generally deserted during early or mid-incubation.

Gadwall breeding home ranges were intermediate in size (average of five = 67 acres) compared to those of other surface-feeding ducks. Shovelers, Cinnamon Teal, and Blue-winged Teal bred on areas estimated no larger than 20 acres. Some pairs of each species usually spent the entire day in full sight from my blind. Mallards and Pintails, on the other hand, ranged so far that I was unable to follow the movements of even a single pair that nested on the study area. Sowls (*loc. cit.*) and Dzubin (*op. cit.*) noted similar interspecific differences in home-range sizes. The reasons for these differences in species mobility are obscure, but appear to be at least partly innate. At Ogden Bay I detected no differences in the habitat requirements of the six species great enough to account for the observed differences in mobility.

Intraspecific intolerance.—Breeding intolerance in surface-feeding ducks is manifest largely in the form of aerial chasing. Aerial pursuits that occur in most species during the nesting season are of two recognizable types—territorial chases and harrying chases. Territorial chases are pursuits in which a mated drake chases the hen of an intruding pair away from his breeding area while the hen's mate follows a short distance behind (Hochbaum, *loc. cit.*; and others). Harrying chases are pursuits in which a group of drakes chases a nesting hen (most commonly an incubating hen) with intent of forcing copulation on her. The exact motivation of these two types of aerial chasing is not clearly understood. Territorial chasing is usually considered an aggressive act concerned with defense of the nesting area or some part of it (Geyr

von Schweppenburg, 1953), or defense of the mated hen, although as Weidmann (1956) suggests, it may actually be motivated by a raping drive similarly involved in harrying pursuits.

Both territorial and harrying chases were observed in typical form in Gadwalls. The former occurred largely during prenesting and egg-laying activities and the latter during incubation, especially after drakes abandoned their mates. I was not able to determine the relationship between the two types of pursuits, but my observations did indicate the nature of territorial chasing in this species and its effectiveness in the spacing of breeding pairs.

Territorial chasing began when the pair established a breeding home range. Chasing was most frequent during the prenesting period. During egg laying and early incubation, chasing normally occurred only when the pair was together, and after mid-incubation, when most drakes deserted their mates, it ceased entirely. Thus the intensity of territorial chasing was related to the presence of the mated hen. Chasing did not appear to be limited to any particular part of the breeding home range. The drake launched his pursuits from any part of the area being occupied by the pair when approached by another pair. That many of a drake's territorial chases originated from only several places, especially the areas most often used for loafing, followed only because the pair spent most of its time together at these sites. From these observations, the territorial chasing of Gadwalls in this study appeared to represent the defense of the mated hen rather than defense of the nesting area. Spatial isolation for the breeding pair appeared to be as effectively achieved in this manner and with far less strife than would have been required to defend the entire breeding home range. Dzubin (*op. cit.*) and others have used the terms "moving territory" and "individual distance" to describe similar drake aggression concerned with defense of mated hens.

Although breeding home ranges apparently were not defended as territories *per se*, territorial chasing was an obvious deterrent to the establishment of late-nesting pairs on the study area. In late May and early June of 1957, the number of nesting pairs on the study area averaged about 35 (Table 3), roughly one pair per 13 acres. Under this density, competition for space was evident. Unattached pairs were frequently driven completely off the study area by the territorial chasing of resident drakes. I once saw a pair chased by five different drakes before it gave up and flew away. Another pair was pursued a total of seven times by four different drakes before it moved on. However, it is not likely that territorial chasing imposed an actual limit to the number of pairs eventually breeding on the area. Generally if a pair persisted in returning to the study area, it finally found a place to feed and loaf unmolested by resident drakes. At the very height of intolerance in late May, I knew of at least six pairs that established themselves on the study area near my

TABLE 4
SITE LOCATIONS OF 156 GADWALL NESTS AT OGDEN BAY REFUGE, 1956 AND 1957
(Data Tabulated by Dates of Nest Establishment)

Site	5 May–5 June	6 June–20 July	Totals
Dikes	30 (39) ¹	19 (24)	49 (31)
Channel banks	41 (53)	34 (43)	75 (48)
Other	6 (8)	26 (33)	32 (21)
Totals	77	79	156

¹ Figures in parentheses are per cent of total nests.

blind despite repeated encounters with other pairs. Hammond and Mann (1956) describe a similar ineffectiveness of Gadwall territorial behavior in limiting the number of pairs nesting under near-colonial conditions on certain islands in North Dakota.

Nest locations.—Early Gadwall nesting was limited largely to channel and dike banks (92 per cent of 77 nests; Table 4) and to dry, upland vegetation dominating these sites (73 per cent of 77 nests; Table 5). Until early June of each nesting season, all but the higher elevations of dikes and the natural levees along channels were either flooded or recently exposed and still wet. More nests were placed in other sites and cover types, notably in the spike-

TABLE 5
COVER LOCATIONS OF 156 GADWALL NESTS AT OGDEN BAY REFUGE, 1956 AND 1957
(Data Tabulated by Dates of Nest Establishment)

Cover type	5 May–5 June	6 June–20 July	Totals	Nests per acre on study area
Upland forbs and grasses ¹	56 (73) ²	33 (42)	89 (57)	1.9
Spike-grass (<i>Distichlis stricta</i>)	6 (8)	22 (28)	28 (18)	0.2
Spike-rush (<i>Eleocharis rostellata</i>)	8 (10)	6 (8)	14 (9)	1.0
Hard-stem bulrush (<i>Scirpus acutus</i>)	2 (2)	7 (9)	9 (6)	0.8
Common cattail (<i>Typha latifolia</i>)	1 (1)	7 (9)	8 (5)	0.1
Rush (<i>Juncus balticus</i>)	4 (5)	3 (4)	7 (4)	1.4
Bayonet-grass (<i>Scirpus paludosus</i>)	0 —	1 (1)	1 (1)	0.1
Totals	77	79	156	

¹ Primarily nettle (*Urtica gracilis*), sweet clover (*Melilotus alba*, *M. officinalis*), aster (*Aster adscendens*), bassia (*Bassia hyssopifolia*), marsh-elder (*Iva xanthifolia*), prickly lettuce (*Lactuca Scariola*), common ragweed (*Ambrosia artemisiifolia*), common sunflower (*Helianthus annuus*), common thistle (*Cirsium* spp.), Junegrass (*Poa pratensis*), brome-grass (*Bromus inermis*, *B. tectorum*) and spike-grass.

² Figures in parentheses are per cent of total nests.

grass flats and in dried stands of cattail and hard-stem bulrush (*Scirpus acutus*), as water levels dropped, but a definite preference for dry sites (79 per cent of 156 nests; Table 4) and upland vegetation (57 per cent of 156 nests; Table 5) was maintained throughout the nesting season. In general, Gadwalls preferred the densest and driest cover available. As a result of the distribution of preferred sites along channels and dikes, 94 per cent of the nests I discovered were within 50 yards of water. Williams and Marshall (1938), Miller and Collins (1954), Bue, Blankenship, and Marshall (1952), and Anderson (1956) recorded similar nesting-cover preferences by Gadwalls.

Other ducks on the study area appeared to be less dependent on dry and/or dense cover for nesting. Pintails, Shovelers, Blue-winged Teal, and Cinnamon Teal most often nested in short, spike-grass cover, 12–18 in. tall, often while this vegetation was still damp underfoot. Mallards appeared to have the widest range of cover tolerances, nesting in all available cover types. I found some Mallard nests in heavy stands of cattail and hard-stem bulrush growing in more than a foot of water.

The concentration of Gadwall nesting on islands with upland vegetation is mentioned by Miller and Collins (*op. cit.*) for Tule Lake and Lower Klamath Wildlife Refuges in California, and by Hammond and Mann (*op. cit.*) for Lower Souris Refuge in North Dakota. I knew of no islands suitable for nesting in northern Utah. However, the concentration of Gadwall nests on elevated sites with upland cover in Utah recorded in the present study and earlier by Williams and Marshall (*op. cit.*) appears to be a result of the same basic preference that accounts for the heavy use of nesting islands on certain marshes where the availability of this preferred cover apparently is more limited.

Clutch sizes.—Completed clutches averaged 10.0 ± 1.3 eggs (70 clutches) in 1956 and 10.1 ± 1.2 eggs (71 clutches) in 1957. Clutch sizes declined during the nesting season as the result of increasing numbers of renests discovered. Renesting attempts almost invariably had smaller clutches than initial nesting attempts (Table 6). Completed clutches in nests I considered to be initial nesting attempts, as explained below, averaged 11.2 ± 1.1 eggs (50 clutches) in 1956 and 10.9 ± 1.3 eggs (42 clutches) in 1957. The two-year mean clutch size for all nests was 10.0 ± 1.2 eggs (141 clutches) and for initial nesting attempts it was 11.1 ± 0.9 eggs (92 clutches).

Nest success.—Of 75 nests located on the study area in 1956, 35 (47 per cent) succeeded in producing one or more hatched chicks. Predation accounted for the failure of 29 nests (39 per cent), desertion 7 (9 per cent), and observer interference 4 (5 per cent). In 1957, I left only 31 nests undisturbed on the area. Of these, 12 (39 per cent) were successful, 15 (48 per cent) were destroyed by predators, and 4 (13 per cent) were deserted. The

TABLE 6

COMPLETED CLUTCH SIZES OF SUCCESSIVE NESTING ATTEMPTS OF 19 MARKED GADWALL HENS AT OGDEN BAY REFUGE, 1956 AND 1957

First clutch	Second clutch	Third clutch	Fourth clutch
12	9		
12	9		
11	10	8	6
11	9		
11	9		
11	9		
11	9		
11	9		
11	8		
11	8	7	
11	8	6	
11	7		
11	8		
10	8		
10	8	7	
10	7		
10	6		
10	5		
9	6		

two-year success rate of all nests was 45 per cent. I observed no nest losses from flooding or other causes.

During the two years of study, predators destroyed 41 per cent of all nests studied and accounted for roughly 80 per cent of all observed, natural nest mortality. California Gulls (*Larus californicus*) and Striped Skunks (*Mephitis mephitis*) are Ogden Bay's only important nest predators. Common Ravens (*Corvus corax*), Black-billed Magpies (*Pica pica*), and Longtail Weasels (*Mustela frenata*) are also present, but in such limited numbers that their importance as nest predators is slight. Of the 44 nests preyed upon in two seasons, I attributed 25 to gulls and 19 to skunks.

On two waterfowl refuges in California, Miller and Collins (op. cit.) reported that 90 per cent of 381 Gadwall nests succeeded. On Bear River Refuge in Utah, Williams and Marshall (op. cit.) reported that 85 per cent of 6,000 Gadwall eggs hatched. In 1947-49, Nelson (pers. comm.) observed a success rate of 73 per cent of 124 Gadwall nests located on my study area at Ogden Bay.

During Nelson's studies, construction of Ogden Bay was still in progress or only recently completed, and nest predators had not yet significantly pop-

ulated the marsh. In contrast, during the present study the refuge sustained high populations of nest predators. Numerous dikes built on the marsh provide ideal skunk-denning sites, and the channel and dike banks, along which duck nests are often concentrated, are used as travel lanes by these predators. Several nesting colonies of California Gulls became established on the refuge following its development, and other gulls from colonies located on nearby islands in Great Salt Lake also forage on the marsh. This increase in predator populations, along with the decline in Gadwall nest success from 73 per cent in 1947-49 to 45 per cent in 1956-57, indicates a possible need for the control of nest predators at Ogden Bay. More will be said of this subject below.

RENESTING

The importance of reneesting in waterfowl productivity was a subject of much speculation, but of little specific study before that of Sowls (1955:129-142). Some of Sowls' more important findings were that reneesting attempts involved smaller clutches, that unsuccessful hens reneested near their original nest sites, and that there were apparent differences in the reneesting abilities of the five species he studied (Mallard, Pintail, Gadwall, Shoveler, and Blue-winged Teal). Sowls' experiments did not permit him to determine the percentage of unsuccessful hens that reneested, but he believed that reneesting was important in maintaining duck populations at Delta.

In my study, I attempted to determine reneesting rates and to measure the amount of annual production contributed by reneesting. Fifty-nine marked Gadwall hens were available for experimentation. Fourteen were 1956 hens, nests of which were destroyed by predators, and 45 were 1957 hens (including 15 originally marked in 1956), nests of which I intentionally disrupted to simulate nest destruction.

Continuous laying.—Four records of re-laying after the destruction of incomplete clutches were obtained. One tagged hen laid a total of 22 eggs in three clutches in 22 days, another laid 12 eggs in two clutches in 12 days, and a third laid 17 eggs in two clutches in 17 days. Each of the three hens moved to new nest sites and resumed egg laying the day after I robbed its nest. I knew of only one laying hen that failed to reneest the day after her eggs were taken. This bird had just laid her tenth egg, possibly completing her clutch, and waited three days to re-lay.

Sowls (ibid.:134-137) pointed out that clutch size becomes fixed sometime before the last egg in a clutch is laid, after which the ovary starts regressing. Continuous laying is possible only prior to that time. Otherwise a renewed period of follicle growth and development, the reneesting interval, must pass before egg laying can be resumed. Sowls found that the reneesting interval lengthened as the stage of incubation at nest destruction advanced. I observed

a similar trend in Gadwalls, although in this study renesting intervals were highly variable after 10 days of incubation. Possibly this variation was due to my inaccurate aging of embryos and back-dating of renests discovered during incubation.

Renest clutch sizes.—Completed clutches in renesting attempts of marked hens averaged 7.8 ± 0.7 eggs (24 clutches), as compared to 10.7 ± 0.6 eggs (19 clutches) in initial nesting attempts (Table 6) (P of no difference < 1 per cent). First nests normally had clutches of 10 eggs or more, and renests had nine eggs or less. Sufficient overlap in clutch size occurred to make it impossible to distinguish renests from first nests with absolute certainty, but the amount of error in such a method obviously was slight (Table 6). For purposes of comparing success rates and hatching sizes of renests with first nests, I considered all clutches of nine eggs or less to represent renesting attempts.

Three laying hens collectively lost clutches of 6, 10, and 11 eggs before I allowed them to finish egg laying. Their completed clutches eventually numbered 11, 10, and 11 eggs, respectively, each of which was normal for first nests. Three eggs were taken from a renesting hen later found incubating a clutch of nine eggs. At least in this small sample, the loss of eggs during egg laying had no apparent effect in lowering the number of eggs in the completed clutch.

Location of renests.—The mean distance between 35 successive nesting attempts of 28 marked hens was only 241 yards, with extreme distances of 110 and 525 yards recorded. The five adult hens whose breeding home ranges are shown in Fig. 3 made a total of 12 known nesting attempts in 1957. Eleven of the 12 nests were situated inside the breeding home ranges of the respective hens as originally plotted during the prenesting and egg-laying periods. From these data, it is obvious that Gadwall hens moved little between nesting attempts. Movements of greater consequence might occur where summer drought or other adverse conditions render an area unsuitable after nesting is already under way. However, the fidelity of Gadwalls for specific breeding areas observed in this study suggests that forced abandonment of familiar nesting terrain might lessen the chances of renesting.

Remating.—Elder and Weller (1954), in a study of domestic Mallards, observed that egg fertility dropped rapidly after hens were isolated from drakes. They concluded that if wild ducks were like tame Mallards, it would be impossible for a hen already abandoned by her mate to reneest and lay fertile eggs without remating. Hochbaum (1944:193) pointed out that bachelor drakes retained their nuptial plumage (and presumably sexual activity) longer than drakes which had obtained mates and had bred. On this basis, Elder and Weller suggested that unbalanced sex ratios in ducks were at least

partly a natural phenomenon. They felt an excess of drakes might be essential to maximum production, since a deserted hen could find a mate and nest again if an earlier clutch was destroyed.

In Gadwalls, desertion by the drake usually occurred before mid-incubation, although I knew of some early nesting pairs that remained together nearly until the time of hatching. Late-nesting and re-nesting pairs appeared to break up soon after the completion of egg laying. Thus the need for re-mating varied seasonally and with the stage of incubation at nest destruction. Eight marked, re-nesting hens were watched specifically for re-pairing, and I knew of only two that did so. However, my observations of these eight hens were limited, and without having marked drakes to study, for evidence of re-mating I had to rely on finding a marked hen paired with a drake whose plumage showed less sign of molt or varied in some other way from that of her original mate's. Accordingly, I am certain that re-mating was more frequent than indicated above.

If excess drakes are essential for successful re-nesting, it may be important to know whether their numbers are sufficient. At the start of nesting, Gadwall sex ratios at Ogden Bay averaged 53 per cent drakes (Fig. 1), or 113 drakes per 100 nesting hens. Data presented in the following section reveal that roughly half of all incubated clutches were unsuccessful, and accordingly at least 50 hens would experience nest destruction sometime during the nesting season. Even considering that some re-nesting hens would still have had original mates, the indicated ratio of 13 unmated drakes per 50 unsuccessful hens appeared inadequate.

Other observations suggested that drakes which had already abandoned their mates might also remate with unsuccessful hens. Gadwall drakes often started molting body feathers before desertion, but obviously retained sexual vigor for a time before becoming flightless. This was apparent in their attentiveness to lone hens, especially in their readiness to participate in harrying chases and the apparent attempted rape of nesting hens. I feel certain that many of them would have paired a second time if given the opportunity. That such matings would be fertile is indicated by Höhn's (1947) finding that spermatogenesis in the Mallard extends into the period of eclipse plumage.

Renest success.—Comparison of the success of renests with first nests is based on 65 nests in 1956 and 26 nests I left undisturbed during re-nesting experiments in 1957. Since renests were distinguished from first nests on the basis of clutch size for unmarked hens, comparisons which follow concern completed (= incubated) clutches only.

In 1956, 25 of 47 first nests and 10 of 18 renests were successful. In 1957, 6 of 14 first nests and 6 of 12 renests succeeded. The two-year success rates of first nests and renests were 51 per cent and 53 per cent, respectively, and

the combined success rate of all incubated clutches was 52 per cent. Although nesting cover was denser and the total amount of cover available for renesting was greater, success of renests was similar to that of first nests.

Data from 1956 and 1957 revealed mean hatches of 8.1 ± 0.7 chicks per successful first nest and 6.6 ± 1.1 chicks per successful reneest.

Renesting rates.—This section of the paper deals with renesting following the destruction of incubated clutches only. That an appreciable number of hens fails to reneest when clutches are destroyed during egg laying is unlikely. Since they have fully developed eggs ready for laying, there is no apparent reason for laying hens not to resume nesting elsewhere. A possible exception to this might occur when nest destruction occurs in the very final stages of egg laying.

In 1957, 45 marked hens were available for study. Nineteen of these originally nested just outside the study area or on the dikes which formed the area's boundaries. Some of the 19 might have reneested outside the area of intensive nest searching, and thus determination of renesting rates is based on the nesting records of 26 hens that originally nested inside the study area, primarily along the main channel (Fig. 3). Conditions for finding nests of these 26 hens were ideal. Breeding home ranges of Gadwalls on the area were sufficiently small that few hens, if any, would have left the area to reneest. In addition, the study area was small enough that all suitable cover could be examined at least once a week during the nesting season, and most of the preferred cover along channel and dike banks was searched every 3 or 4 days. An indication of the efficiency of nest searching is provided by the fact that only 8 of 22 renesting attempts had progressed beyond 12 days of incubation when discovered. For these reasons I believe very few nests were missed. Nonetheless, renesting rates presented below probably should be considered minimal values.

Of the 23 experimental hens that lost incubated first clutches, 74 per cent made second nesting attempts, and of the 19 that lost incubated second or third clutches, 26 per cent reneested again. Fifty-two per cent of all hens experiencing nest destruction during the entire course of renesting experiments in 1957 was known to reneest (Table 7).

Chi-square values for tests of independence in 2×3 contingency tables for renesting versus the stage of incubation at nest destruction and the number of clutches previously produced were 7.79 (P of independence < 2.5 per cent) and 9.34 (P of independence < 1 per cent), respectively. Thus the ability to reneest declined as the stage of incubation at nest destruction advanced. In addition, it was lower after the loss of reneest clutches than first clutches.

TABLE 7
RENESTING RECORDS OF 23 MARKED GADWALL HENS AT OGDEN BAY REFUGE, 1957

Days of incubation at nest destruction	Per cent of hens reneesting			Totals
	After loss of first clutch	After loss of second clutch	After loss of third clutch	
1-6	92 (12) ¹	50 (6)	50 (2)	75 (20)
7-12	67 (6)	14 (7)	0 (2)	33 (15)
13-18	40 (5)	0 (2)	— (0)	29 (7)
Totals	74 (23)	27 (15)	25 (4)	52 (42)

¹ Figures in parentheses are sample sizes.

During reneesting experiments in 1957, 6 hens tagged in 1956 (adults) made a total of 14 nesting attempts, 2.3 per hen, as compared to 17 hens tagged in 1957 (unaged; adults and juveniles) that made a total of 34 nesting attempts, 2.0 per hen. This difference falls short of statistical significance, although I suspect adult hens were more persistent reneesters than juvenile hens. Since adult hens were found to be among the earliest pairs to begin nesting, a longer period of time apparently is available to them for reneesting. More extensive field observations than were made in this study might verify the hypothesis that adults are more persistent in reneesting.

In Table 8, which is based on natural nest success rates from 1956-57 and on reneesting rates determined by experimental nest predation in 1957, reneests account for 29 per cent of the total reproductive effort. In 1956, 65 nests with completed clutches were discovered on the study area. Of these, 18 (28 per cent) were known reneests or considered to be reneests on the basis of clutch size. Since the success of incubated clutches in 1956 (54 per cent) was

TABLE 8
PRODUCTION OF A HYPOTHETICAL POPULATION OF 100 GADWALL HENS FROM DATA
OBTAINED AT OGDEN BAY REFUGE, 1956 AND 1957
(Calculations Carried out through Fourth Nesting Attempt)

Nesting attempt	Number of hens	Renesting rate	Clutches started	Success of incubated clutches	Successful clutches	Young per clutch	Total young produced
1	100	—	100	0.52	52	8.1	421
2	48	0.74	36	0.52	18	6.6	138
3	18	0.27	5	0.52	3		
4	2	0.25	0	0.52	0		
Totals			141		73		559

similar to that used in Table 8 (52 per cent), the similarity in amounts of re-nesting indicates that the over-all re-nesting rate determined by experimentation in 1957 also prevailed under conditions of natural nest mortality in 1956.

Re-nesting abilities appeared to vary considerably between the several species of ducks nesting on the study area. Observations of the comparative time span of nesting activities led me to believe that Mallards and Pintails were more persistent re-nesters than Gadwalls, and that Blue-winged Teal and Cinnamon Teal were much less persistent. Sowls (*op. cit.*:139-141) also noted interspecific differences in re-nesting abilities. Of the five species he investigated (Mallard, Pintail, Gadwall, Shoveler, and Blue-winged Teal), he considered the Pintail the most persistent re-nester and the Blue-winged Teal the least persistent.

Importance of re-nesting.—The contribution of re-nesting to Gadwall production in this study is evident in Table 8 in which a hypothetical breeding population of 100 nesting hens experiences the various production rates observed in this study. In this calculation, 559 young are produced at hatching, 421 (75 per cent) from initial nesting attempts, and 138 (25 per cent) from re-nesting attempts. The contribution of re-nesting is substantial. Total production of young at hatching is a third greater than might be expected without any re-nesting. In the absence of re-nesting, success of incubated clutches would have to be a third higher (69 per cent versus 52 per cent) to net the same production of young.

BROODS

Movements.—Thirty-five Gadwall broods hatched on the study area in 1956, but only three spent major portions of their rearing periods there. The net movement of Gadwall broods at Ogden Bay was from the heavily used upland nesting areas, on which all but channels and ditches became dry by mid-August, to deep-water marshes and the edges of large impoundments. Broods belonging to 13 marked hens were located after they left the study area. The distances they had traveled from where they hatched varied from 0.26 to 1.15 miles, averaging 0.56 mile.

Brood sizes and mortality.—Data from 1956-57 showed a mean hatch of 7.5 ± 0.8 young from 52 successful nests. Brood counts during the two years revealed means of 6.8 ± 0.7 for 121 Class I broods, 6.3 ± 0.7 for 139 Class II broods, and 5.8 ± 0.9 for 57 Class III broods. I observed no evidence of brood combination in broods of marked hens. According to the system of age classification used in this study (Gollop and Marshall, 1954), Class I Gadwalls (downy) are 1-18 days old, Class II (partly feathered) are 19-44 days old, and Class III (fully feathered but incapable of flight) 45-50 days

old. These data suggest an over-all mortality rate of 23 per cent between hatching and time of flight, with approximately 43 per cent of the indicated mortality taking place in the first 18 days of life. A similar shrinkage of 23 per cent in Gadwall broods was observed on another Utah marsh by Odin (1957). California Gulls were the only serious predators on young ducks at Ogden Bay (cf Odin, *ibid.*).

DISCUSSION

Production versus mortality.—Table 8 shows 100 nesting hens producing 559 chicks at hatching, 280 of which can be assumed to be females. About 77 per cent, or 215 young hens, would survive to the age of flight and self-sufficiency. Application of survival rates calculated in Table 1 (48 per cent for adults; 33 per cent for juveniles) shows, on the average, 48 adult hens alive at the start of the following nesting season and 71 juvenile hens alive a year later (late summer). Since some mortality of juvenile hens undoubtedly occurs during the nesting season, the number of juveniles surviving at the start of nesting would be somewhat more than 71, and thus the total number of breeding hens would be somewhat greater than 119. Accordingly an increase in nesting hens in excess of 19 per cent is indicated.

Annual breeding-pair inventories at Ogden Bay, however, show populations of 255, 244, 317, 257, 217, 189, 210, 208, 215, and 205 pairs for the successive years 1950–59 (Nelson, 1950–1959), demonstrating that the refuge population of Gadwalls has, in fact, remained fairly stable, at least since 1954. Apart from sampling errors, at least three conditions may be involved in this discrepancy, each of which might be important in evaluating the results of the present study: (1) Survival rates, calculated from 1929–53 banding, may not have applied to Ogden Bay Gadwalls during the period of study. (2) Production data were gathered on a study area aggregating less than 5 per cent of the entire marsh and may not have applied to the refuge population at large. That nearly 20 per cent of Ogden Bay's Gadwalls nested on this small area in 1956–57 demonstrates the area's attractiveness and suggests that nesting conditions there may have been more favorable than on other parts of the marsh. (3) If in reality production has outweighed mortality in recent years, a limit may exist in the number of breeding Gadwalls Ogden Bay can accommodate under present conditions. In view of the high rate of homing of adult hens observed in this study, the net loss of breeding stock to other areas probably would comprise a disproportionate number of juvenile hens.

Renesting and nest success.—In the population of Gadwalls studied, actual production of young at hatching was a third higher than might have been expected in the absence of renesting. A difference of this magnitude implies that renesting is an important factor in the ability of this population to main-

tain itself. It is obvious, however, that renesting cannot offset all nest mortality. Had nest success rates of 73 per cent observed on my study area in 1947–49 by Nelson (pers. comm.) applied to the population I studied in 1956–57, production would have been at least 25 per cent higher (701 versus 559 young at hatching). That the productivity of Ogden Bay Gadwalls has, indeed, dropped with declining nest success, in spite of what appears to be a high level of renesting, is indicated by Nelson's (loc. cit.) breeding-pair censuses which show an average of 268 pairs for 1950–53, as compared to an average of 207 pairs for 1954–59.

The decline in Gadwall nest success at Ogden Bay has been shown to correspond to a period of increasing nest-predator numbers on the marsh. A question thus arises concerning the advisability of predator control. No definite answers can be given in the absence of prior information on the costs and effectiveness of possible control measures. However, I believe that the evidence is sufficiently conclusive to justify experimental control, the results of which should be evaluated over a period of several years before a final recommendation is made.

In general, results of this study seem to indicate that even with persistent renesting, serious production losses are likely to occur if nest mortality is excessive. In this connection, measures to improve low nest success on areas that can be managed for nesting ducks probably should not be overlooked in the belief that renesting can offset high nest-mortality rates. This may apply particularly to such species as the Blue-winged Teal and Cinnamon Teal, suspected of being less persistent renesters than Gadwalls, and to areas having importantly lower nest-success rates than observed in this study.

SUMMARY

In 1957, resident Gadwalls arrived at Ogden Bay in mid-April. At least 60 per cent of the surviving hens marked in 1956 returned in 1957 and nested in the immediate vicinity of their 1956 nest sites. Egg laying started nearly a month after spring arrival. This delay was believed to be typical for northern Utah and may have resulted from the Gadwall's dependence on dry and dense cover for nesting.

Gadwall breeding-pair behavior followed the pattern of home-range occupancy described by Sowls (1955) and Dzubin (1955). Breeding home ranges averaged 67 acres in size. Home ranges were shared by two or more breeding pairs. Territorial behavior was apparently concerned with defense of the mated hen instead of defense of the nesting area and was observed to be ineffective in limiting the number of pairs nesting on the study area.

Seventy-nine per cent of all nests studied were situated on elevated sites provided by dike banks and natural levees, and 57 per cent were located in upland vegetation. Nest success for all nests was 45 per cent in 1956–57, compared to 73 per cent in 1947–49. Success of incubated clutches during the study was 52 per cent. Predation was responsible for 80 per cent of all observed, natural nest mortality in 1956–57. Completed clutches

for all nests averaged 10.0 ± 1.2 eggs in 1956-57, and completed clutches in initial nesting attempts averaged 11.1 ± 0.9 eggs.

Completed clutches in renesting attempts of marked hens averaged 7.8 ± 0.7 eggs, compared to 10.7 ± 0.5 eggs in initial nesting attempts. The success of renests, 53 per cent, was similar to that of first nests, 51 per cent. Unsuccessful hens renested near their original nest sites. Fifty-two per cent of all hens experiencing experimental loss of incubated clutches were known to renest. The ability to renest dropped as the stage of incubation at nest destruction advanced and was lower after the loss of renest clutches than first clutches.

Renesting accounted for 25 per cent of Gadwall production during the study, but fell considerably short of compensating for increased nest mortality since 1947-49. On this basis, experimental control of nest predators at Ogden Bay was recommended.

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UTAH COOPERATIVE WILDLIFE RESEARCH UNIT, UTAH STATE UNIVERSITY, LOGAN, UTAH, 17 MARCH 1961 (PRESENT ADDRESS: WISCONSIN CONSERVATION DEPARTMENT, BOX "D," HORICON, WISCONSIN)

NEW LIFE MEMBER

Fernando C. Novaes, an active member of the WOS since 1953, has now become a Life Member. He is a Biologist-Associate in Ornithology with the Departamento de Zoologia—Secretaria da Agricultura, of São Paulo, Brazil; and has done museum work in Rio de Janeiro and Pará, taking many trips on the Amazon. Mr. Novaes is interested primarily in systematics and population ecology of birds, and has published about 20 papers in *The Auk*, *Condor*, *Revista Brasileiro Biologia*, and local journals. He is also a member of the AOU and the Cooper Ornithological Society.

